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4. Continental Shelf Food Chains of the Northern Gulf of Mexico

Abstract

Biological productivity in the northern Gulf is significantly affected by the Mississippi River. The freshwater discharge (577 km^3 yr^{-1}, approx 10% of the volume of water on the shelf) contains high concentrations of dissolved nutrients (100-150 μmol NO$_3$ l^{-1}). Flow is primarily constrained by prevailing winds to the continental shelf west of the Mississippi Delta. River plumes are regions of high phytoplankton stock (>30 g Chl l^{-1}) and production (5 g C m^{-2} d^{-1}), high copepod stocks (nauplius concentrations >1000 l^{-1}) and high ichthyoplankton stocks (larval concentrations >50 m^{-3}). The high temperature of shelf waters assures high physiological rates, implying high rates of trophic transfer and high turnover rates. The primary fate of phytoplankton production is grazing by macrozooplankton and microzooplankton. However, sinking of phytoplankton and other organic material fuels the annual development of a band of hypoxic water along the Louisiana coast. Fisheries production is high; the northern Gulf supports the largest volume fishery in the United States, the Gulf menhaden, *Brevoortia patronus*. The Loop Current in its northernmost position affects shelf processes to the east of the Delta. Anticyclonic rings derived from the Loop Current occasionally impact on the Louisiana shelf west of the Delta but usually drift over to the western Gulf resulting in exchange of oceanic and shelf water off Texas.

Introduction

The morphology of the shelves of the northern Gulf of Mexico is relatively simple (Figure 4.1). DeSoto Canyon is the easternmost boundary of the region. The shelf break occurs near the 100-m isobath which lies 100-150 km offshore east of the Mississippi River
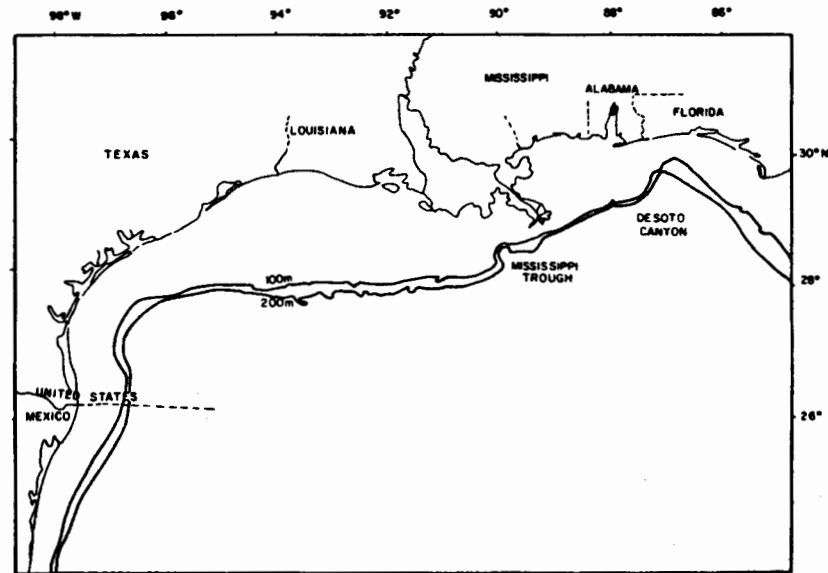
Figure 4.1. The northern Gulf of Mexico with bathymetry simplified to emphasize the broad shallow continental shelf of the region.

Delta. The Delta has built out nearly to the shelf break causing the shelf to narrow abruptly as one approaches the Delta. West of the Delta, a small canyon-like feature, the Mississippi Trough, cuts across the shelf and may represent a region of preferential off-shelf transport of particulate material. Further west, near 92°W, the shelf broadens to a width of approximately 200 km and then narrows again westward. Offshore of the Texas coast, it turns gently southward as one approaches the Mexican border.

The northern Gulf of Mexico is highly productive biologically. Portions of the shelf affected by the Mississippi River discharge have long been noted as regions of high phytoplankton stocks and productivity (Riley, 1937; El-Sayed, 1972). Phytoplankton production rates in excess of 5 g C m^{-2} d^{-1} have recently been reported in Mississippi River plume waters (Lohrenz et al., 1990; Ortner et al., submitted). There is evidence that zooplankton productivity is also high in the northern Gulf of Mexico (Dagg et al., 1987; Ortner et al., 1989) and fisheries production is very high. For example, the gulf menhaden, *Brevoortia patronus*, supports the largest volume fishery in the United States (Warlen, 1988).

Several factors suggest that the Mississippi River system is the ultimate source of much of the biological productivity on the Louisiana/Texas shelf: the river discharge is large and much of it remains on the broad shallow shelf for several months; river waters contain high concentrations of dissolved nutrients; and the open Gulf of Mexico does not appear to be a significant source of shelf nitrogen, although little is known about shelf/slope exchanges in this region.

The purpose of this paper is to present an initial characterization of the shelf environment of the northern Gulf of Mexico, and to indicate some of the processes that support the high biological production of this region.

Physical Regime

The dominant forcings of the shelf circulation are the strong runoff signal due to the Mississippi River system and the seasonally varying local meteorology. The Mississippi River system runoff averages 577 km^3 yr^{-1}. Much of this occurs during the spring flood, and average daily discharge during the fall is only about 30% of the springtime high. Less than one third of the discharge flows eastward onto the Mississippi/Alabama shelf; most of the water discharging through the Mississippi River delta flows westward. About one third of the total system discharge enters the Gulf through the Atchafalaya River system and Atchafalaya Bay.

The summer breezes tend to be weak and southerly or southeasterly with characteristic time scales of the order of a few weeks. Occasional tropical storms and hurricanes represent significant disturbances to the area, particularly where they strike directly. During the fall, the summer winds weaken and the influence of cold air outbreaks from the north and northwest are felt on time scales of three to ten days. Latent heat loss is extensive and wave action over the shallow inner shelf is severe. Wind-driven set-up of a meter or more causes strong flooding of the adjacent wetlands and significant estuarine-shelf exchange (Schroeder and Wiseman, 1986). The role of these cold air outbreaks is dominant throughout the winter and early spring.

The relative strengths and timings of these weather and runoff variations influence the circulation and stratification of the shelf waters. These effects are better understood for the West Louisiana/ Texas shelf than for the Louisiana/Mississippi/Alabama shelf. Therefore, this article primarily focuses on the shelf west of the birdfoot delta.

Due to buoyancy, water emanating from the major passes of the birdfoot delta of the Mississippi River rapidly separates from the bottom. It forms a well-defined plume with strong frontal boundaries

which are regions of significant shear and convergence. The halocline beneath the plume breaks down through wind-mixing and shear instability (Wiseman et al., 1976a; Wiseman et al., 1976b). Local tides modulate the flow from the mouth of the river thereby affecting the entire plume structure and its associated fronts. The low salinity water emanating from the multiple river mouths and crevasses in evanescent plumes merges to form an identifiable flow of low salinity water which is traceable from the region of the Delta and which attaches to the coast within a few tens of kilometers downstream (Wiseman et al., 1982). A low salinity coastal boundary layer results and flows westward along the coast (Cochrane and Kelly, 1986). Variations in the velocity of this flow are driven by the winds on time scales of the synoptic weather patterns. The salinity of these waters is lowered by the effluent from the small coastal rivers, bayous and bays and by the major influx of river water from Atchafalaya Bay. The waters of the coastal boundary layer exchange efficiently with the local estuarine waters and are important to recruitment processes (Shaw et al., 1985). They are separated from the mid-shelf waters by a strong salinity front. Cross-frontal exchange processes are important to the transport of larvae and nutrients, but none of the mechanisms involved have been studied in detail.

Normal Fickian diffusion is probably weak in such a strongly stratified situation. Satellite imagery has shown examples of effluent plumes from estuaries traversing the front during cold air outbreaks. While such a process might take low salinity waters into the inner and mid-shelf regions, it appears to be a uni-directional process. Hydrographic surveys occasionally suggest meso-scale eddies forming along the front and possibly separating from it (Figure 4.2). During cold air outbreaks, the isopycnals in the front are more nearly vertical than during more weakly forced situations. It is not clear whether the altered density pattern is an advective response to wind forcing or whether the pycnocline breaks down due to mechanical mixing. The latter possibility would cause an efficient two-way exchange of shelf and coastal boundary layer waters. Finally, there exist regions of enhanced vertical mixing along the inner shelf such as the shoals immediately offshore of the Atchafalaya Bay (Chuang and Wiseman, 1983). It is possible that the majority of exchange across the front occurs in these regions. Cross-frontal exchange is an important process and clearly is worthy of further study.

Following the spring runoff maximum, the coastal boundary layer can be traced as far as the Mexican border and recent observations suggest that it remains an identifiable feature well into Mexican waters (Figure 4.2). In the late spring and early summer, winds along the Mexican and south Texas coast become upwelling favorable while those over the Louisiana coast remain downwelling favorable. (Indeed, weak upwelling along the south Texas coast
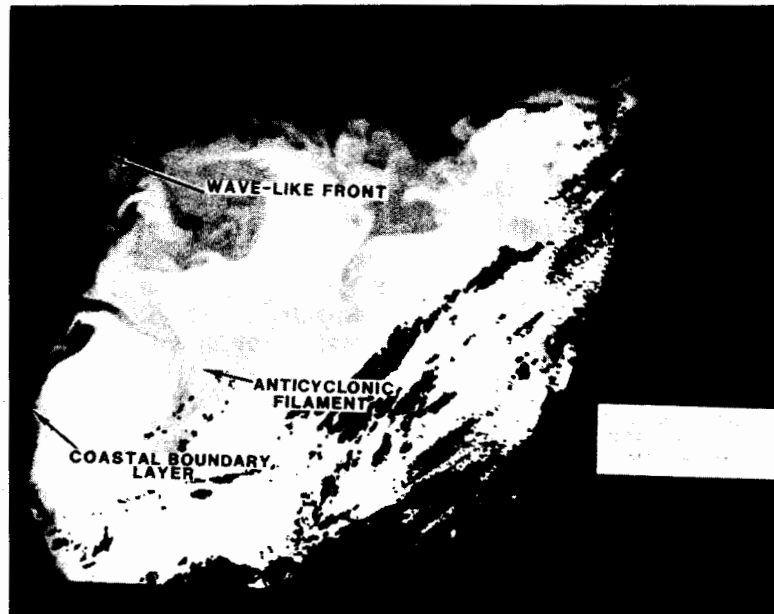
Figure 4.2. AVHRR image of the northwestern Gulf of Mexico for 3 March 1988. Land and clouds have been masked in black. Colder waters are represented by darker colors. Note: (1) the penetration of a cold coastal boundary layer into Mexican waters, (2) wave-like features on the frontal boundary of the coastal boundary layer in Texas waters, and (3) shelf break exchange as cold water is drawn offshore and rotates around an anticyclone in the western Gulf. (Courtesy of L. J. Rouse, Jr.).

appears to have been observed in hydrographic data [Cochrane and Kelly, 1986]). More importantly, the coastal boundary layer in this region changes flow direction. Waters return upcoast to the north and east along the Texas coast. A convergence zone develops and the low salinity waters flowing westward are turned offshore. This convergence zone migrates northeastward until mid-summer. Later, as the summer wind systems weaken, the southward flowing coastal boundary layer redevelops all along the Texas coast.

Under the weak summer winds, a strong halocline isolates the deeper nearshore waters from direct air-sea exchange. A region of severe near-bottom hypoxia develops along much of the Louisiana coast most years (Rabalais et al., in press). During winter storms, strong mixing vertically homogenizes the water column and reaerates the lower layer. A strong salinity front, though, still isolates the inner shelf waters from the mid-shelf waters. Between cold air outbreaks, when winds are weaker, a halocline may develop but it disappears with the arrival of the next cold front.

Wind forcing is normally a strong control on shelf circulation. Over the Texas/Louisiana shelf, though, direct wind forcing appears to leave a large portion of the subtidal current variance unexplained. Empirical orthogonal function analysis of existing data suggests that about half the subtidal variability is directly driven by the local winds. It is not clear what drives the remaining variability. Subtidal variance of the current field is large and seasonal mean currents estimated from direct measurements are often statistically insignificant.

Over the outer shelf and upper slope, Cochrane and Kelly (1986) posit a quasi-permanent, upcoast (eastward) current. The small number of direct current measurements available all indicate eastward flow in this region. Furthermore, the dynamic topography at the sea surface with respect to 70 db generally indicates eastward flow. The dynamics responsible for generating such a flow remain an enigma. The dynamic low which Cochrane and Kelly identify over the mid-shelf results in part from air-sea interaction occurring during winter cold air outbreaks. Cold, dry polar continental air flows out over the shelf and massive latent heat fluxes to the atmosphere occur (Nowlin and Parker, 1974). The salinity structure is such that the cooling produces denser water at mid-shelf than is found either inshore or further offshore. Some of this dense water sinks and runs downslope carrying with it dissolved material and material resuspended by wave-bottom interaction during the cold air outbreaks (McGrail and Carnes, 1983). The remainder comes into geostrophic equilibrium and contributes to the low in dynamic topography found over the shelf (Cochrane and Kelly, 1986).

Shelf break exchange is an important process but the studies necessary to fully document and explain it in this region have not yet been carried out. Offshelf flow, either into Mexican waters or into the deep Gulf, required to balance the freshwater budget of the shelf has been estimated (Dinnel and Wiseman, 1986) although the processes involved were not indicated. As mentioned above, along the south Texas shelf, the winds are upwelling favorable during much of the late spring, summer, and early fall. Other processes, though, appear to contribute as well.

Rings which break off from the Loop Current in the northern Gulf of Mexico typically migrate in a southwesterly direction and enter the western Gulf. Some, in contrast, move directly westward through the northern Gulf and interact with the slope west of the Delta. These anticyclonic rings are often associated with smaller cyclonic features. The circulation of the cyclones and anti-cyclones are observed, on AVHRR and CZCS imagery, to entrain chlorophyll laden shelf waters off the shelf (T. Leming, personal communication) (Figure 4.2). Concurrent surveys indicate that these waters also have increased ichthyoplankton concentrations. A final shelf break
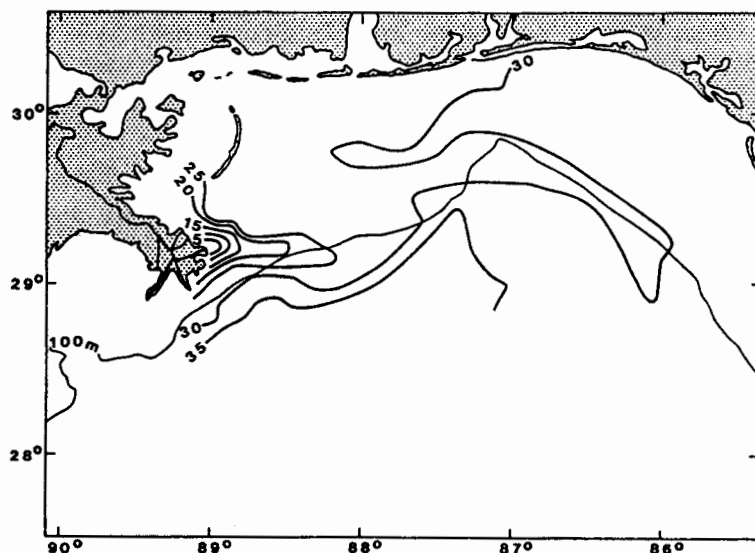
Figure 4.3. Sea surface salinity pattern east of the Mississippi River delta for 29 June-3 July 1964. Note the tongue of low salinity water characterized by the 30 $^\circ/_{oo}$ isohaline, which flows along the shelf break. (Redrawn from Drennen, 1968).

exchange process, mentioned above, occurs during winter months when heavy water forms at mid-shelf, sinks, and flows seaward (McGrail and Carnes, 1983).

East of the Mississippi River Delta, the shelf circulation is again strongly influenced by the Mississippi River discharge as well as by the fresh water discharge of the Mobile, Pascagoula and Pearl Rivers. A strong halocline is often present across the shelf. Mississippi River waters are usually found to flow eastward along the shelf break as a distinct low-salinity surface feature (Figure 4.3). Inner shelf, low-salinity waters flow westward, but are strongly wind-driven and respond to the seasonal and subtidal wind changes (Dinnel, 1988; Chuang et al., 1982).

To our knowledge, there is no current meter data from the mid-shelf region east of the Delta in the public domain. The U.S. Minerals Management Service is presently sponsoring a field program to collect such data. When it is available, it should enhance our knowledge of the circulation in this region.

Shelf waters are often entrained into the offshore by deep Loop Current intrusions into the northeastern Gulf (Schroeder et al., 1987; Huh et al., 1981). Dinnel (1988) has also hypothesized the existence of two regions of preferential offshore transport, one into the

northwest portion of DeSoto Canyon and the other at approximately 88°W. Both of these regions are identified from mean hydrography and may only exist in a statistical sense. The role that such offshore transport of nutrient laden Mississippi discharge may play in the trophic dynamics of the open Gulf has recently been discussed (Walsh et al., in press).

Another important shelf break exchange process in the region east of the delta is wind-driven during the winter months. Southerly and southeasterly winds force water into the corner region formed by the Delta and the Mississippi coastline. As these winds relax, the water flows southward along the Delta and the Chandeleur Islands and crosses the shelf break immediately east of the Delta (Hart and Murray, 1978; Schroeder et al., 1985).

There is a potential for communication across the Delta front. Long-term current meter measurements in front of the Delta do not suggest a statistically significant mean flow except during periods when the Loop Current may be deeply intruded into the Gulf (Wiseman and Dinnel, 1988). Nevertheless, the subtidal oscillations in the flow field are energetic and of long period. Thus, the time-varying component of the flow may well be capable of transporting material across the Delta front.

Nutrient Inputs

The discharge waters of the Mississippi River system are a major source of dissolved nutrients for the shelf of the northern Gulf of Mexico. The annual discharge west of the delta is equivalent to approximately 10% of the volume of water on the entire Louisiana/Texas shelf out to 90 m (Dinnel and Wiseman, 1986), and nutrient concentrations in river waters are high; nitrate concentrations often exceed 100 μmol l^{-1} (Dagg and Whitledge, 1991). Indeed, if no other factor were limiting and riverine input of nitrate was uniformly distributed over the entire shelf, it would be sufficient to support "new" phytoplankton production of 30 g C m^{-2} y^{-1} (Table 4.1; Dagg and Whitledge, 1991). Patterns of nitrate use are of course not uniform. Rather, nitrate is stripped from the water within a short distance from the input sources (river discharge points), typically less than 100 km (Dagg and Whitledge, 1991; Ortner et al., submitted).

Because a significant fraction of the water in the coastal boundary layer originates from the river discharge plumes, these waters often contain high concentrations of dissolved nutrients. Exchange between the coastal boundary layer and the mid-shelf waters provides nutrients for mid-shelf production. An example of such an exchange was observed during a period of strong northerly and westerly wind during February 1984 when waters from the

Table 4.1. Potential stimulation of "new" production by the annual nitrate input to the Louisiana-Texas Shelf west of the Mississippi River delta. (From Dagg and Whitledge, 1991.)

Freshwater input[a]	382×10^9 m^{-3} y^{-1}
Nitrate concentration[b]	100 mg-at m^{-3}
Shelf area to 90 m[a]	10686 km^2
Nitrate input	3.57×10^2 mg-at m^{-2} y-1
Nitrogen input	50×10^2 mgN m^{-2} y-1
C equivalent (assumes C:N=6)	30 g C m^{-2} y^{-1}

[a]Dinnel and Wiseman (1986).
[b]Walsh et al. (1981) and Turner et al. (1987) suggest 150 mg-at m^{-3}. Concentrations in 1935 of less than 15 mg-at m^{-3} were reported by Riley (1937).

coastal boundary layer were displaced offshore at the surface by nutrient-poor upwelled water (Dagg, 1988).

High concentrations of dissolved nutrients are observed in subsurface and bottom waters of the mid-shelf region, particularly in areas strongly affected by discharge plumes during periods of the year when shelf waters are stratified, suggesting significant benthic regeneration of dissolved nutrients (see below). Processes by which these nutrients are supplied to the euphotic zone are not well studied in this region but permanent salt driven stratification around the discharge plumes suggests significant horizontal transport along the shelf usually must occur prior to winter overturn.

Processes that result in the exchange of shelf and slope waters are not likely to be a significant source of dissolved nitrogen for shelf production processes. Waters of the open Gulf of Mexico are typically impoverished of nitrate (<1 μmol l^{-1}) to a depth of 75-100 m throughout the year (references in Walsh et al., in press; Murrell and Dagg, 1987; Toon and Dagg, 1989). Nitrate concentrations equal to those often observed in bottom waters of the mid-shelf off Louisiana are not observed in open Gulf waters until depths of several hundred m are reached. Shelf-slope exchanges of water must primarily be viewed as contributing to nutrient losses from the shelf in this region. Quantification of these exchanges is not possible at this time.

One type of event that may cause significant exchange of shelf and slope or open Gulf waters is the abuttment of rings that break off from the Loop Current onto the outer shelf. Remote imagery indicates that these rings entrain shelf waters (Figure 4.2). As indicated above however, the nutrient concentrations of replacement waters are likely to be low.

Upwelling favorable winds off the Texas coast during summer, winds that reverse the flow of the coastal boundary layer, suggest that offshore water containing some significant source of dissolved nutrients might stimulate phytoplankton production on the Texas shelf. The existence of enhanced phytoplankton biomass in a bottom nepheloid layer between the coast and out as far as 70 m during summer (Kamykowski and Bird, 1981) is consistent with this view, although enhanced nutrient concentrations within the nepheloid layer were not observed.

Phytoplankton

The northern Gulf of Mexico is characterized by strong frontal boundaries, at the interface between river discharge plumes and receiving shelf waters, at the interface between the coastal boundary layer and mid-shelf waters, and at the interface between the outer-shelf waters and the open Gulf. Remotely sensed patterns of chlorophyll distribution in the northern Gulf of Mexico illustrate that surface phytoplankton stocks are highest within the discharge plumes of the Mississippi and Atchafalaya Rivers, and within the coastal boundary layer. Concentrations in mid- and outer-shelf waters are higher than those of the open Gulf. Concentrations in the shelf waters off Texas are generally lower than those of the Louisiana shelf. Regions of mixing and exchange between coastal waters and mid-shelf waters are indicated by enhanced offshore concentrations of surface phytoplankton. Similar frontal processes are observed at the shelf/slope boundary (Heron et al., 1989).

High levels of primary production in the northern Gulf of Mexico have been attributed to the input of new nutrients from the Mississippi River (Riley, 1937; Thomas and Simmons, 1960). However, the dynamic and heterogeneous nature of the Mississippi River plume (Lohrenz et al., 1990; Ortner et al., submitted) has complicated attempts to relate changes in levels of riverine nutrient inputs to corresponding changes in regional primary production. Nutrients (e.g., Riley, 1937; Boynton et al., 1982) and light (e.g., Pennock and Sharp, 1986; Cloern, 1987) are thought to be the principal factors regulating phytoplankton dynamics. Observations of initial limitation of production by light and subsequent limitation by nutrient supply along decreasing turbidity gradients in estuaries might be expected to apply to river plumes (e.g., Xiuren et al., 1988). Indeed, the spatial pattern of high production and biomass at intermediate salinities in the northern Gulf of Mexico (Figure 4.4) encourages such speculation. Further evidence comes from observations that water column light attenuation in the Mississippi River
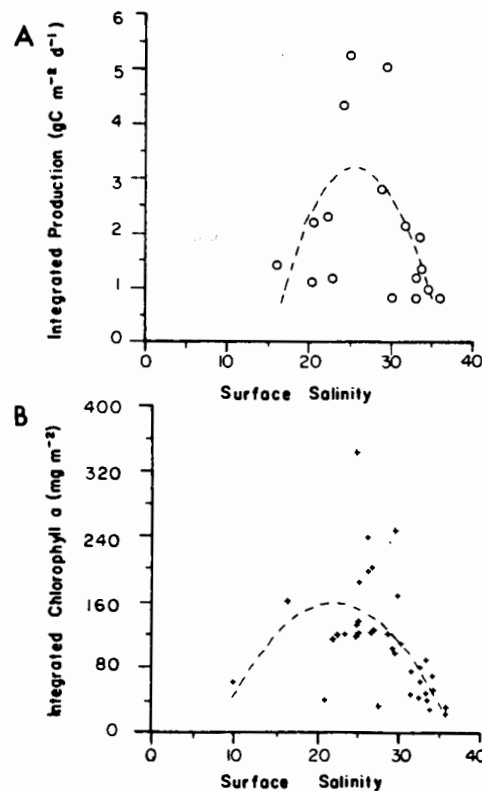
Figure 4.4. Phytoplankton productivity vs. salinity, near the Mississippi River delta during April 1988: [14] C primary production (A) and Chlorophyll *a* (B) integrated over the entire water column in relationship to surface salinity. (From Lohrenz et al., 1990).

plume was inversely related to nutrient concentrations along the salinity gradient (Lohrenz et al., 1990).

The hypothesis that primary production is light-limited in turbid areas of the Mississippi River plume was tested by Lohrenz et al. (1990) during an April 1988 study. The investigators found that a major proportion (>80%) of the spatial variation in production was accounted for on the basis of light and chlorophyll levels, supporting the view that light was an important controlling factor. However, a light-limitation model (Wofsy, 1983; Lohrenz et al., 1990) indicated light conditions in the surface mixed layer of the plume were adequate to support phytoplankton concentrations greater than were observed, even at the most turbid stations (Figure 4.5). These researchers suggested that factors in addition to light (e.g., sinking,
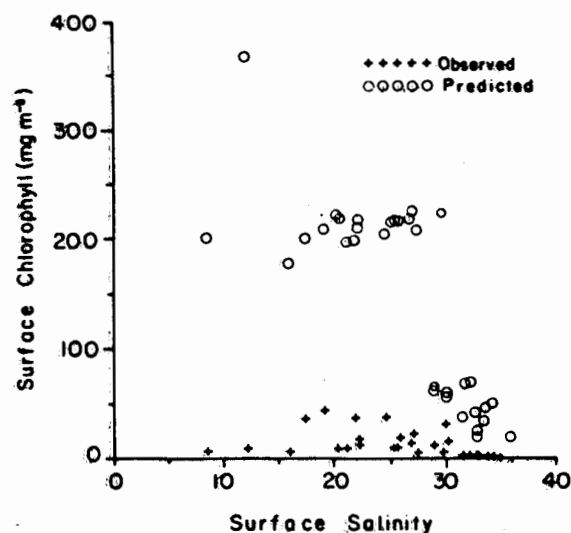
Figure 4.5. Comparison of observed surface Chlorophyll *a* concentrations with those predicted from Wofsy (1982) model as described in Lohrenz et al. (1990) plotted versus surface salinity.

grazing, physical dilution) contributed to regulation of phytoplankton concentrations, and hence primary production. Ortner et al. (submitted) found no evidence for shade adaptation in phytoplankton populations sampled from the base of the euphotic zone in areas of high turbidity during September 1982, supporting the view that phytoplankton growth may not be light-limited in the plume. Moreover, they estimated growth rates of 3-5 doublings d^{-1}, close to the maximum for phytoplankton at 28°C (Eppley, 1972).

In addition to uncertainties regarding the role of light in influencing production in turbid eutrophic areas, there are questions as to mechanisms of nutrient limitation in adjacent shelf waters. Concentrations of dissolved silicate and nitrate have been reported near detection levels (e.g., Shiller and Boyle, 1987; Lohrenz et al., 1990) and both nutrients have been suggested as limiting to phytoplankton along the plume/oceanic gradient (Sklar and Turner, 1981; Thomas and Simmons, 1960). It may be that different nutrients limit different taxonomic groups of phytoplankton (i.e., silica for diatoms and nitrogen for others). There are at least two distinct phytoplankton communities associated with the Mississippi River and Gulf of Mexico that mix to varying degrees in the plume (Thomas and Simmons, 1960). Phytoplankton from the Mississippi River are probably not limited by the same factors as phytoplankton from the

Gulf. In fact, even within the same community, different species may be limited by different factors.

It is clear that more work is needed to define relationships between regional primary production and Mississippi River nutrient inputs, and to determine the factor(s) which limit phytoplankton growth and production in northern Gulf of Mexico waters. Riley (1937) acknowledged the possibility that factors other than light and nutrients may contribute in regulating phytoplankton distributions in the northern Gulf of Mexico. The importance of other controlling factors has been subsequently noted in other coastal ecosystems (Pennock, 1985; Fransz, 1986).

Factors besides light and conventional nutrients which may play an important role in influencing primary production in the northern Gulf of Mexico include the high metal concentrations associated with the Mississippi River outflow (Shiller and Boyle, 1987). The toxicity of copper is well-known (e.g., Sunda and Guillard, 1976; Fitzwater et al., 1982), although the possible complexation of trace elements by organic matter in the plume would diminish effective toxicity. An additional factor which could inhibit phytoplankton growth is the steep gradient in salinity. Variations in salinity may significantly influence photosynthesis and growth of phytoplankton species (e.g., Smayda, 1969; Miller and Kamykowski, 1986a). Such effects may occur on relatively short time scales (Miller and Kamykowski, 1986b). These observations lead to the view that in areas of dynamic estuarine circulation, growth and production may be suppressed due to salinity variations.

Another potential impact of large changes in salinities would be loss of some species from the community (Filardo and Dunstan, 1985; Jackson et al., 1987). Such transitions may result in a lag as marine species colonize the newly mixed waters, and would significantly affect sinking characteristics of the phytoplankton community. Riley (1937) suspected an inhibitory effect of low salinity on phytoplankton in the Mississippi River plume, which could be explained by such a process. The combination of phytoplankton population and environmental changes can also affect grazer community characteristics (Dagg et al., 1987; Ortner et al., 1989).

Spatial and Temporal Patterns

Preliminary estimates of mixed layer integrated production suggest consumption of nutrients by phytoplankton production was comparable to riverine inputs within spatial scales of <100 km (Lohrenz et al., 1990). From these estimates, it was concluded that the ecosystem of the plume environs is eutrophic, with an abundant supply of new nutrients and production limited by other factors. As distances from the outflow region increase, the role of heterotrophic

nutrient regeneration will likely become more important. Turner et al. (1987) noted that primary production beyond the plume is primarily nitrogen limited, and hypothesized that increases in riverine nutrient inputs result in increased inputs of phytoplankton carbon to bottom waters in those areas.

Data adequate to resolve seasonal patterns in phytoplankton production are currently lacking for the northern Gulf. However, in view of the large changes in river flow and corresponding nutrient outputs, seasonal variation in the extent of the river-influenced region is likely to be substantial (e.g., Fucik, 1974; Sklar and Turner, 1981). In addition to variation in the magnitude of freshwater and nutrient inputs, changes in ratios of nutrients may alter responses of the phytoplankton community. Also, seasonal variations in river-borne materials, such as dissolved organics and suspended particulates, could alter optical conditions in the plume (e.g., Sathyendranath et al., 1989; Lohrenz et al., 1990). Seasonal changes in temperature are also likely to influence ecosystem dynamics. Lower temperatures during winter months may constrain rates of primary production, as well as hetero-trophic consumption (Boynton et al., 1982).

Phytoplankton Fates

Zooplankton Grazing

As pointed out recently by Ortner et al. (1989), little work has been done on zooplankton of the northern Gulf of Mexico. It has been well documented in other regions however, that species composition changes across shelves. Hopkins et al. (1981) showed this is the case for copepods on a transect of the west Florida shelf into the open Gulf; epipelagic species of copepods show farthest landward distribution while deeper dwelling forms remain more oceanic. Based on examination of three regions, Ortner et al. (1989) concluded there was a gradient in copepod species composition in the northern Gulf of Mexico between the estuarine community and the open Gulf community. Species characteristic of the shallow low salinity waters were *Acartia tonsa, Temora turbinata, Labidocera nerii, Centropages furcatus, Paracalanus quasimodo, Farranula carinata,* and *Temora stylifera.* Species characteristic of deeper more saline waters of the open Gulf of Mexico included *Eucalanus attenuatus, Phaenna spinifera, Candacia pachydactyla, Calanus minor, Eucalanus elongatus,* and *Calanus tenuicornis.* Because discharge waters from the Mississippi River frequently override oceanic waters in the vicinity south of the Mississippi Delta, species of the deep ocean community are often found beneath the estuarine community associated with the river plume. In addition, there is a distinct

community in transition waters (as represented by samples from Cape San Blas, Florida), which included *Oithona plumifera*, *Corycaeus clausii*, *Oncea mediterranea*, *Oncea venusta*, and *Candacia curta*. Up to 87% of the total macrozooplankton numbers in the nearshore regions were copepods. Waters of the coastal boundary layer are likely to primarily contain the species of the "shallow, low salinity water" community of Ortner et al. (1989). Several years of collecting non-quantitative zooplankton samples for experimental work in coastal waters south of LUMCON support this expectation; the low salinity water community is most common, with occasional contributions from the transition community (Dagg, 1988; Dagg, unpublished observations). *Acartia tonsa* is typically the most abundant macrozooplanktonic species in estuarine areas of the northern Gulf of Mexico (Lesley, 1977; McIlwain, 1968), and observations from low salinity shallow waters near the Atchafalaya River mouth and from the Mississippi River plume indicate the *Acartia tonsa* is the dominant copepod in these waters (Dagg and Walser, submitted; Dagg, unpublished observations).

Evidence suggests that zooplankton production is high in the northern Gulf of Mexico. The highest individual sample biomass and copepod abundances measured by Ortner et al. (1989) were in the low salinity surface waters of the Mississippi River outflow, and concentrations of copepod nauplii are typically higher in the region around the Mississippi River Delta than in waters of similar depth and distance from shore farther to the east and west of the Delta in Florida and Texas (Dagg et al., 1987). Concentrations of nauplii away from the plume, in high salinity waters, were lower in all seasons than concentrations in the intermediate salinity range of the plume waters.

Limited data also suggest a strong seasonal pattern in the stocks of zooplankton, at least in the low-salinity community. Ortner et al. (1989) noted that springtime zooplankton stocks in the Mississippi River region were much higher than wintertime stocks. Similarly, concentrations of copepod nauplii in plume waters of the Mississippi River were between 10-100 l^{-1} during wintertime cruises (Dagg et al., 1987), between 50 and 100 l^{-1} during an April cruise (Dagg and Whitledge, 1991), and up to 1600 l^{-1} during a summer cruise (Dagg and Whitledge, 1991).

These limited data suggest a strong seasonal cycling of macrozooplankton stocks in the discharge plumes and probably in coastal and shelf waters influenced by river discharge. Such a cycle suggests that grazing by the macrozooplankton community is also strongly seasonal.

In a series of papers (see Turner, 1987 and references therein), Turner describes by SEM the contents of fecal pellets collected from common copepod species feeding in natural water from locations near the Mississippi River Delta. Collections were made during wintertime.
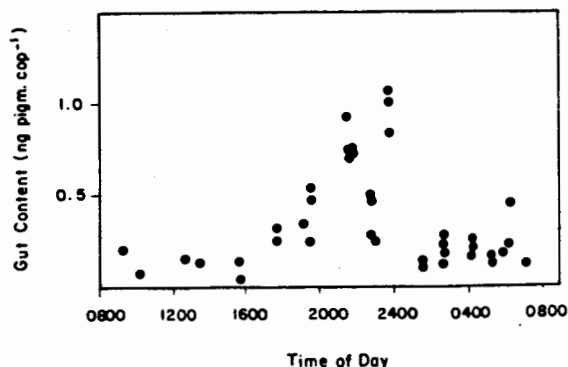
Figure 4.6. Level of phytoplankton pigments observed in the copepod *Acartia tonsa* from the Atchafalaya River discharge into Fourleague Bay during May 1989. Note the strong diel signal.

In most of the species he examined, including *Acartia tonsa*, *Paracalanus quasimodo*, *Temora turbinata*, *Temora stylifera*, and *Eucalanus pileatus*, pellet contents reflected the phytoplankton contents of the ambient water. In addition, copepods collected from highly turbid plume waters produced pellets containing large numbers of inorganic particles. Some species, including *Centropages velificatus* and *Labidocera aestiva*, contained crustacean remains in addition to phytoplankton remains and inorganic particles, indicating a more omnivorous diet. These studies are of interest but do not provide quantitative information on the feeding rates of these copepods.

Preliminary measurements of ingestion by *Acartia tonsa* adult females from Fourleague Bay (a bay receiving Atchafalaya River water at the head and Gulf of Mexico water at the mouth) were made during May 1989 (Figure 4.6). Ingestion of phytoplankton was 28.3 ng Chl d^{-1} during this 24 h sampling cycle, with most of the feeding occurring at night. Assuming a population density of 30 adults l^{-1}, commonly observed in Fourleague Bay (Dagg, unpublished), yields a total ingestion of 0.85 mg Chl m^{-3} d^{-1}. Chlorophyll stocks in surface waters at this time were 10-15 mg m^{-3}. Immature stages of *Acartia* greatly outnumbered adults at this time and would have contributed significantly to the total ingestion by this species of copepod. Therefore, the *Acartia tonsa* population probably ingested 20-30% of the phytoplankton stock daily during this period. Similar measurements for copepod populations in waters of the Mississippi River plume and Louisiana shelf have not been made but high copepod densities suggest that macrozooplankton grazing is an important source of phytoplankton mortality in these regions.
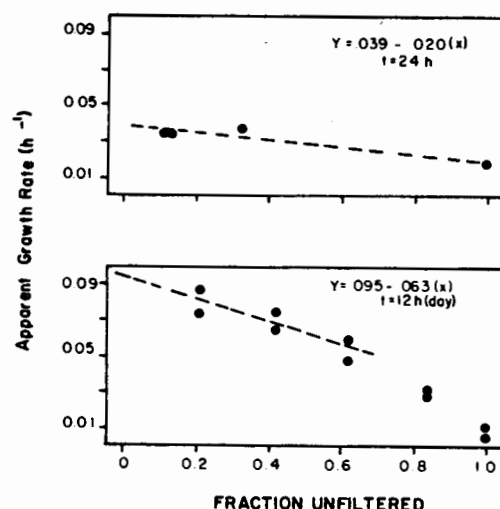
Figure 4.7. Grazing rates of the microzooplankton community from the Atchafalaya River discharge into Fourleague Bay during May 1989 (upper panel) and September 1989 (lower panel). Non-linearilty in the September experiment is attributed to nutrient limitation during the incubation.

Composition of the microzooplankton community in the northern Gulf of Mexico has not been documented. Some initial characterization was done by Gifford and Dagg (1988) in Terrebonne Bay, a coastal environment characterized by intermediate salinities, high phytoplankton concentrations and a macrozooplankton community dominated by *Acartia tonsa*. High concentrations of unicellular microzooplankton, including tintinnids, aloricate ciliates and zooflagellates, were observed during the summer and lower concentrations in the winter. During the summer, microzooplankton comprised a significant fraction of the diet of *Acartia tonsa* (Gifford and Dagg, 1988).

Preliminary measurements of ingestion by the microzooplankton community have been made in both Atchafalaya and Mississippi plume waters (Dagg, unpublished). During May and September 1989, the microzooplankton community ingested 38% and 53% (Figure 4.7) of the phytoplankton stock d^{-1}, respectively, in the region of the Atchafalaya River discharge. Similar, high, rates of ingestion by the microzooplankton community were observed in the Mississippi River plume during September 1989 (Dagg, unpublished). These experiments although preliminary, indicate the microzooplankton community is very active especially during the summer in the northern Gulf of Mexico.

In summary, macro- and microzooplankton grazing crop significant portions of the phytoplankton community in coastal and shelf waters of Louisiana. Losses are probably greater during the spring and summer than during the winter. Direct comparisons of phytoplankton mortality due to the total grazing by both communities with phytoplankton growth or productivity measurements are required.

Grazing on phytoplankton by the macrozooplankton community has additional consequences for the shelf ecosystem. A copepod defecates about 30% of the phytoplankton it ingests; the remainder is recycled (as CO_2 for carbon and primarily as NH_4 for nitrogen) or synthesized into new tissue as growth or reproductive products. Strong seasonality in grazing by macrozooplankton would significantly affect the flux of material to the bottom. If, as limited data suggest, winter and early spring are periods of comparatively low grazing mortality for phytoplankton, then direct sinking of phytoplankton cells to the benthos could dominate the vertical flux. In comparison, during the summer and fall when macrozooplankton stocks are high and grazing by the macrozooplankton community is a large source of mortality for the phytoplankton, little direct sedimentation of phytoplankton cells would occur and the dominant flux component would be copepod fecal pellets.

Fecal pellets are a major component of sinking particles beneath the plume of the Mississippi River during spring and fall (Nelson and Trefry, 1986). Summer fluxes of pellets would likely be even greater. Fecal pellet concentrations of $>1.5 \times 10^6$ m^{-2} have been observed in bottom samples on the Louisiana shelf (Dortch, pers. commun.). A population of only 10 adult *Acartia* spp. l^{-1} in river plume waters could produce 5×10^6 pellets m^{-2} d^{-1}.

Phytoplankton losses to microzooplankton grazing are more complete. Fecal remains from ingestion processes of microzooplankton organisms are small and effectively do not sink (Welschmeyer and Lohrenzen, 1985). Microzooplankton rapidly recycle a large fraction of the particulate carbon and nitrogen they ingest (Goldman et al., 1985). Ingested material partitioned to growth is thought to be quickly consumed by other microzooplankton components of the microbial food web and thereby mostly recycled (Azam et al., 1983), or ingested by macrozooplankton (Gifford and Dagg, 1988).

In summary, phytoplankton ingested by the microzooplankton community is primarily recycled within the water column, and the microzooplankton community contributes little to the flux of particulate material to the benthos. In contrast, approximately one third of the phytoplankton carbon and nitrogen ingested by the macrozooplankton community may reach the bottom as fecal pellets. This may have important implications for fueling near-bottom

hypoxia, commonly observed during the summer in coastal waters of Louisiana (Rabalais et al., in press) and for the long-term fate of particulate carbon.

The high concentrations of nitrate entering the Gulf at the Mississippi River mouth are physically diluted and biologically stripped from the water within a comparatively small distance, <100 km (Dagg and Whitledge, 1991). Within this zone the phytoplankton community is dominated by large diatoms (Ortner et al., 1989; Turner, 1987 and references therein), and it is probable that a large fraction of the phytoplankton production is supported by "new" nitrogen (primarily nitrate but also some ammonium) input from the river. Macrozooplankton grazing is probably highest within this region. Vertical flux of particulate material, either live phytoplankton cells or copepod fecal pellets, is likely to be large. Outside of this zone of direct utilization of riverborne nitrogen, phytoplankton production decreases (Lohrenz et al., 1990) and is likely increasingly dependent on recycled nitrogen. The phytoplankton community is typically dominated by small cells, and microzooplankton grazing is likely predominant. Vertical flux of particulate material is small because particles, both phytoplankton cells and microzooplankton fecal pellets, are small. By implication, the same patterns would be observed near the Atchafalaya River mouth.

Sinking

Phytoplankton sinking is expected to be especially important in circumstances where the rapid response of phytoplankton to sudden introduction of new nutrients exceeds that of the zooplankton grazers. An example is the sedimentation of the spring diatom bloom in coastal areas (Platt and Subba Rao, 1970; Skjoldal and Lannergren, 1978). High phytoplankton sinking rates are also associated with nutrient depletion (Titman and Kilham, 1976; Fahnenstiel and Scavia, 1987) and with cells of high density (i.e., diatoms). Because diatoms appear to be the dominant phytoplankton assemblage in the Mississippi River plume and adjacent shelf regions (Thomas and Simmons, 1960; Fucik, 1974; Q. Dortch, pers. commun.) and nutrient availability varies tremendously across this gradient, losses through phytoplankton sinking may be significant. Evidence that phytoplankton sinking does occur comes from direct observations of intact cells on the sediment surface in the area (Q. Dortch, pers. commun.). High sediment pigment values, which have been associated with periodic low oxygen events to the west of the delta (Turner and Allen, 1982; Rabalais et al., in press), provide additional evidence for high rates of sedimentation of photosynthetically produced organic matter.

Deposition and Burial

Coastal and shelf sediments can be significant reservoirs of organic materials and nutrients that are deposited but not regenerated to the water column. The distinction in time scales between temporary versus permanent storage of particulate material in bottom sediments is important in determining the ultimate fate of materials in shelf ecosystems. The terms used to describe sedimentation on various time scales can be distinguished quantitatively using radiochemical techniques for establishing geochronologies within bedded sediments, and for examining rates of sedimentary processes. Deposition is the temporary emplacement of particulate material on a sediment surface. Burial (accumulation) is the sum of deposition and removal over a longer time scale (McKee et al., 1983). Within an environment, the magnitude of benthic nutrient processes (sedimentation and regeneration) depends on the time scale of interest.

The relative magnitude of burial is controlled by the quantity and quality of particulate material supplied to bottom sediments (Zeitzschel, 1980; Klump and Martens, 1983). Direct empirical relationships have been established between high sedimentation rates and the burial of organic nutrients (Toth and Lerman, 1977; Suess, 1980). A substantial proportion of the particulate material delivered to coastal ecosystems is supplied by a few large rivers such as the Mississippi/Atchafalaya system. In river-dominated shelf environments, areas with highest particle deposition rates are usually dominated by relatively refractory terrigenous materials (Aller et al., 1985). Using a transport-reaction model, Aller and Mackin (1984) hypothesized that the maximum loss of a given nutrient by burial occurs when $D_sK = W^2$, where D_s is the sediment mixing coefficient (dominated by bioturbation), K is the first-order decomposition rate constant for the organic fraction, and W is the deposition rate. On any time scale, it is the relationship between deposition and decomposition that determines the magnitude of particulate nutrient storage in bottom sediments.

The input of freshwater to land-margin ecosystems leads to the formation of density fronts that enhance sedimentation and lead to high inputs of nitrogen, phosphorus and organic matter to bottom sediments. A common observation in river-dominated environments is that most of the sediment discharge is initially deposited near the river mouth and sedimentation rates decrease with increasing distance from the source (DeMaster et al., 1985; Nittrouer et al., 1987). Therefore, a decrease in deposition rates from proximal to distal portions of dispersal systems is likely, especially during high flow periods when riverine discharge dominates. From high flow to low
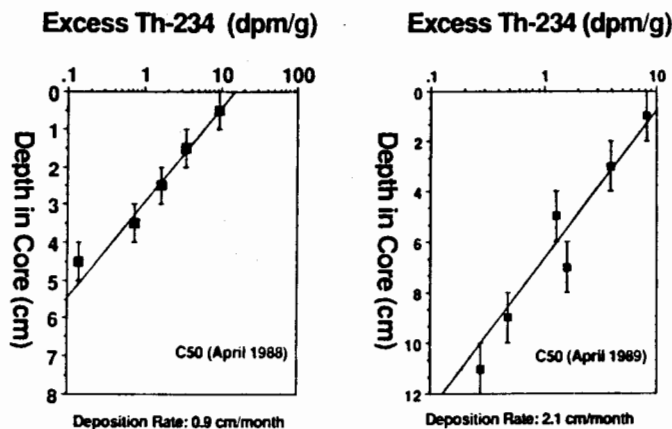
Excess Th-234 (dpm/g)

Figure 4.8. Particulate deposition rates at a shelf site (50 m water depth) proximate to Southwest Pass of the Mississippi River as determined by [234]Th geochronology. The deposition rate during April (high river-discharge) of the "dry" year, 1988, was a factor of two less than the deposition rate at the same site for April of a "normal" year, 1989.

flow periods, Mississippi River discharge decreases by about 85%, resulting in reduced riverine input to the shelf and leading to a more uniform dispersal of particulates throughout the dispersal system.

In a temporally variable environment such as this, a seasonal measure of particulate deposition may be much more important to understanding patterns of benthic nutrient regeneration and loss of nutrients via sedimentation than a measure of long-term accumulation rates that integrate over several decades. Net nutrient storage in bottom sediments is a balance between deposition and regeneration. The combination of high deposition rates and low sediment reactivity should result in a proportionally higher temporary storage of particulate nutrients, especially in the proximal portion of the dispersal system. Deposition in the more distal portions is dominated by reactive organic matter from phytoplankton and thus decomposition and regeneration in these regions may be higher.

Sediment cores collected from the shelf adjacent to the Mississippi River were analyzed for naturally occurring [234]Th and ^{210}Pb, to quantify sedimentary processes on time scales ranging from months to years (Figures 4.8 and 4.9, McKee et al., 1990). The absence of macrobenthos near the river mouth results in the preservation of primary sedimentary structure. Therefore, the distribution of [234]Th and ^{210}Pb in the seabed is controlled by sedimentation and these naturally occurring radionuclides can be used

Excess Pb-210 (dpm/g)
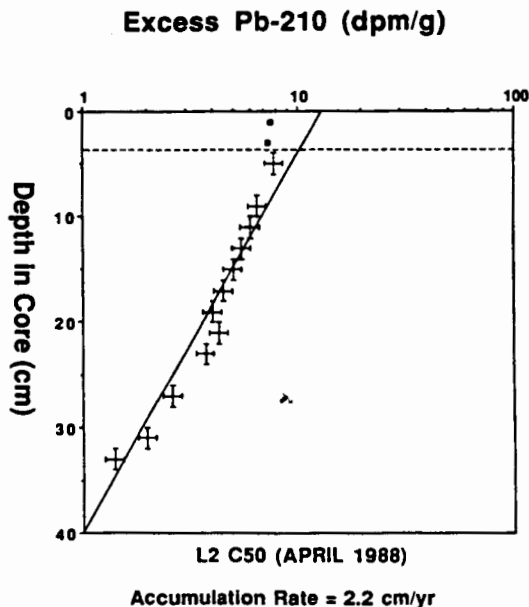

L2 C50 (APRIL 1988)

Accumulation Rate = 2.2 cm/yr

Figure 4.9. The rate of particulate accumulation (deposition minus removal) at the 50-m shelf site as determined by ^{210}Pb geochronology. This rate integrates over a period of approximately 100 years, and is a factor of 6 to 12 times less than deposition rates measured at this site.

to quantify sedimentation rates. Using ^{234}Th, sediment deposition rates (100-d time scale) were measured during the high river-discharge stage of two successive years. In 1988 (an unusually dry year in the Mississippi River basin), sediment deposition during the high river-discharge period was 0.90 cm/mo (Figure 4.8 upper panel). In 1989 (a "normal" year), the deposition rate was 2.10 cm/month, a factor of two higher (Figure 4.8 lower panel). Deposition rates (100-d time scale) at this site are 5-10 times greater than sediment accumulation rates (100-yr time scale) determined using ^{210}Pb (Figure 4.9). Therefore, the relative rates of deposition, redistribution and burial in the study area may vary on time scales of days to decades.

In addition to measurements of the quantities of organic matter that are deposited in bottom sediments, some estimate of the biological reactivity (quality) of the organic matter is needed to determine its potential for decomposition/remineralization. In other regions, lignin and carbohydrate analyses of particulate organic matter collected in sediment traps and in bottom sediments of a coastal

marine bay have been used to determine the relative fluxes and reactivities of terrigenous and marine-derived organic matter (Hedges et al., 1988). These investigators concluded that about 67% of the organic carbon flux was marine derived, but that only about 33% of the organic matter in the bottom sediments was of marine origin. Thus, marine-derived organic matter was several-fold more reactive than terrigenous materials and contributed most significantly to benthic and water-column nutrient regeneration. Even though terrigenous organic matter is not as biologically reactive as its marine counterpart, the recycling of a small portion of the annual discharge of the Mississippi River (4 X 10^{12} g C; Malcolm and Durum, 1976) would have a major impact on coastal ocean productivity.

Benthic Remineralization

The contribution of nutrient remineralization from sediments to water column production of phytoplankton in shelf ecosystems is significant. In the North Sea, 75% of the nitrogen requirements are met by benthic regeneration (Billen, 1978), and in the Kiel Bight this flux may provide 100% of the phytoplankton demand for nutrients (Zeitzschel, 1980). Walsh et al. (1978) estimated that sediments contributed 38% of the total nitrogen regeneration in the Mid Atlantic Bight, equivalent to the regeneration by zooplankton in the water column. Rowe et al. (1975) suggested that sediments in shallow shelf ecosystems such as in the New York Bight, may provide "more than the total required nitrogen." In a later analysis, regenerated nitrogen in the Mid Atlantic Bight during the summer of 1980 was found to provide 50-80% of nitrogen productivity although the contribution by sediments was estimated to be only 7% of the total nitrogen regeneration (Harrison et al., 1983). Direct measurements of benthic ammonium flux in Christiansen Basin and stations in the New Jersey and Long Island shelf regions average 71 and 105 μmol m^{-2} h^{-1}, respectively (Rowe, 1978). Ammonium flux from sediments in the shelf off the mouth of the Changjiang River, East China Sea, ranged from -108 to 142 μmol m^{-2} h^{-1}, with an average of 29 μmol m^{-2} h^{-1} (Aller et al., 1985). Wide variation is observed in rates of benthic nitrogen regeneration in shelf ecosystems but it appears that benthic regeneration of nitrogen in most shelf ecosystems is about half that observed in shallow land margin systems such as estuaries (e.g., Boynton and Kemp, 1985; Nixon, 1981).

Fluxes of nutrients and dissolved oxygen across the sediment-water interface of the Louisiana shelf ecosystem are within the upper range of rates for most shelf ecosystems (Figure 4.10). These remineralization rates are based on measurements at 9 stations in the shelf region near the vicinity of the Mississippi River plume, during August 1987, April 1988, and April 1989. Rates of ammonium
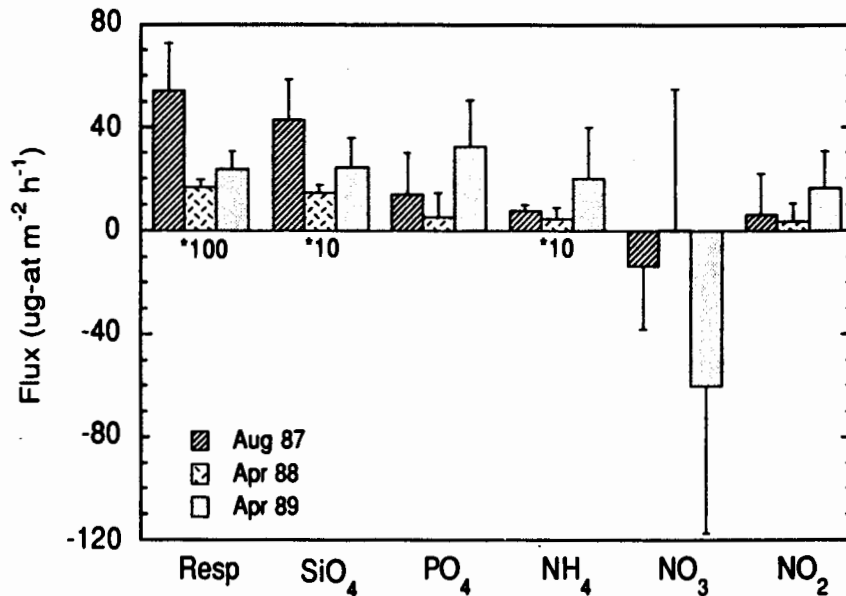
Figure 4.10. Rates of exchange of dissolved oxygen, silicate, phosphate, ammonium, nitrate, and nitrite across the sediment-water interface in a Louisiana shelf ecosystem.

regeneration ranged from 75-200 μmol m^{-2} h^{-1}. Lohrenz et al. (1990) have estimated phytoplankton demand for nitrogen (2.0 x 10^7 g N d^{-1}) based on models of primary productivity in a 1700 km^2 region of the Louisiana shelf in April 1988. Using a mean flux of 200 μmol m^{-2} h^{-1} of ammonium from sediments during this period, we calculate that benthic remineralization could contribute about 40% (0.8 x 10^7 g N d^{-1}) of the phytoplankton demand for nitrogen in this system. The contribution of sediments may be even higher in summer when river nutrient input is lower and benthic remineralization rates are higher. Thus in the Louisiana Shelf Ecosystem, sediments may be significant in sustaining high rates of primary productivity during the summer when allochthonous input is low.

Benthic nutrient remineralization is proportional to the quantity and quality of organic nutrients deposited to the benthos, and is influenced by in situ production rates (e.g., Hargrave, 1973; Klump and Martens, 1983) and by the density of animal burrows in sediments. A close association between riverine nutrient input and sediment regeneration has been observed in the Louisiana shelf. Large differences in remineralization rates, attributed to differences in river discharge, were observed between April 1988 and 1989

(Figure 4.10). River discharge was lower in 1988, resulting in less input of materials to the seabed. Regeneration rates of silicate, phosphate, and ammonium were all lower in 1988 than 1989, a near normal river discharge year (Figure 4.10). Based on models by Toth and Lerman (1977) and sedimentation rates ranging from 2-5 cm yr^{-1} on the Louisiana shelf (McKee, pers. commun.), ammonium regeneration rates should range from 51-128 μmol m^{-2} h^{-1}, similar to the range observed from direct measurements of sediment processes.

In river-dominated coastal environments, sedimentation of terrigenous materials and associated water column turbidity dilute the labile or reactive organic matter reaching bottom sediments and inhibit in situ production of particulate material in the overlying water column (DeMaster and Nittrouer, 1983; Aller et al., 1985). The reactivity (relative to decomposition) of bottom sediments in these environments is inversely proportional to sedimentation rate and rates of benthic nutrient remineralization may differ spatially due to the reactivity of deposited material (Blackburn, 1980; Aller et al., 1985). Thus maximum rates of ammonium and silicate benthic regeneration occurred off the shelf from the Changjiang River in areas of lower deposition. Rates of benthic regeneration of ammonium and silicate in the Louisiana shelf region are generally higher near the mouth of the Mississippi River, yet maximum flux is sometimes observed downstream from the river plume. Both ammonium and silicate show a significant correlation with pigment content in sediments, indicating the importance of the quality of material to rates of benthic regeneration.

Denitrification may also represent a loss of nutrients from marine ecosystems and reduce the potential of nitrogen regeneration. The theoretical ratio of particulate material in the water column according to Redfield (1958) is 106C:16N:1P. Stoichiometric signals of elements buried in the sediment that vary from this theoretical ratio can be used to model processes that selectively operate on nitrogen relative to phosphorus in pore waters (Grundmanis and Murray, 1977). Stoichiometric models of estuaries have concluded that benthic remineralization of organic matter yields inorganic nitrogen and phosphorus fluxes back to the water column which are low in nitrogen relative to phosphorus, and low in nitrogen relative to depositing organic matter. For example, material deposited to sediments in Narrangasett Bay had N:P ratios of 13.3, yet the ratio of sediment remineralization was 3.8 to 7.5 (Nixon, 1981). This shift in the N:P ratio of regenerated nutrients is caused by denitrification and significantly impacts the metabolism of marine ecosystems (Seitzinger et al., 1980). Yet the influence of denitrification and burial have not been interpreted relative to patterns of nitrogen regeneration from sediments.

Denitrification has not been directly measured in sediments of

the Louisiana shelf. However, using stoichiometric models, the fluxes of dissolved oxygen, ammonium and phosphate across the sediment-water interface can be used to estimate this process. Based on the measured release of phosphate from sediment and a N:P ratio of 16, the expected flux of ammonium is 277 μmol m^{-2} h^{-1}. However, the measured rate is only 108 μmol m^{-2} h^{-1}, suggesting that nitrification is occurring at 169 μmol m^{-2} h^{-1}. Assuming that all except for the nitrite released from sediment is denitrified, and adding the sediment nitrate uptake rate, total denitrification is 185 μmol m^{-2} h^{-1} (86% of which is from coupled nitrification/ denitrification). The proximal portions of shelf systems in Louisiana are characterized by high concentrations of nitrate and here maximum rates of sediment uptake and denitrification should occur (Twilley and Kemp, 1986). From a mass balance perspective, this loss of nitrogen is nearly equivalent to that which is regenerated and represents a significant flux of nitrogen in this shelf ecosystem.

Fishes of the Northern Gulf of Mexico

Fishes of the northern Gulf of Mexico are generally considered by zoogeographers to be warm temperate (Carolinian), with close affinities to the ichthyofauna along the U. S. east coast from Cape Hatteras to about Cape Canaveral. There is considerable faunal change with depth and season, with tropical species being more common on the deeper portions of the continental shelf and juveniles of tropical species appearing throughout the northern Gulf during the warmer season (Briggs, 1974).

Some species are resident, relying upon resources within the northern gulf to successfully complete their life cycles, while other species are migratory and occur only seasonally in the northern gulf. Migratory species are able to take advantage of ephemeral resources that are seasonally available for adult feeding, or food and shelter of young stages.

Any of several ecological criteria (e.g., trophic position, habitat requirements, reproductive strategy, etc.) may be used to construct categories of estuarine dependent, coastal, reef and oceanic species.

Estuarine Dependent Species

The estuarine dependent group includes the Gulf menhaden, southern flounder, red drum, spot, Atlantic croaker, spotted sea trout and striped mullet. The life history pattern for this group typically involves spawning in neritic waters followed by transport of larvae and young juveniles to estuaries. Larval survival and recruitment to estuaries is dependent to a large extent upon oceanographic and

meterological conditions (e.g., Nelson et al., 1977; Checkly et al., 1987). Many of these species feed at relatively low trophic levels in the estuaries, and tend to be more abundant than coastal species which frequently prey heavily upon them. However, important sources of variability in recruitment to the adult stock may also be present during the estuarine phase of the life history, when physical factors, food abundance and other habitat characteristics cause considerable variation in growth and mortality.

Perhaps the best studied species in this group is the Gulf menhaden, *Brevoortia patronus*. It has a relatively short food chain consisting on one or two trophic levels. Spawning takes place on the continental shelf during fall and winter (Shaw et al. 1985) and the pelagic larvae are transported into estuarine nursery areas in 6-10 wk (Deegan and Thompson, 1987). Juveniles and adults are filter feeders. The food repertoire changes with age from a predominantly herbivorous to a more omnivorous diet, with a wide size overlap (Friedland et al., 1984). Young larval Gulf menhaden feed on phytoplankton and zooplankton, especially dinoflagellates, tintinnids and copepod eggs, while older larvae eat larger zooplankton, including juvenile pelecypods, pteropods and copepod nauplii, copepodites and small adult copepods (Govoni et al., 1983). Juveniles may consume primarily detritus of marine macroplytes in estuaries (Lewis and Peters, 1984), and adults apparently feed on both large phytoplankton and zooplankton (Durbin, 1979). The extraordinary productivity of this species (it supports the largest fishery by weight in the U. S.) is partially accounted for by its short food chain, and partially by the highly productive environments, offshore and estuarine, in the northern Gulf of Mexico.

Coastal Species

The coastal group is comprised of a large number of ecologically and economically important species, including king mackerel, Spanish mackerel, bluefish, coastal herrings, little tuny, crevalle jack, blue runner, butterfish and hakes. The most important shared characteristic of this group is that members complete their life cycles in the pelagic or benthic realm associated with the continental shelf. Most are high trophic level predators, usually piscivores, as adults and juveniles. Most spawn pelagic eggs in marine waters, and although some species opportunistically inhabit or feed in estuaries, particularly as juveniles (e.g., bluefish and Spanish mackerel), none are strictly estuarine dependent. Principal spawning areas and factors that may determine reproductive success and ultimate recruitment are little known. Because spawning is in continental shelf waters, major oceanographic phenomena such as geostrophic current boundaries or eddies and riverine fronts may offer key habitats for successful

reproduction and recruitment (e.g., Kirobe, 1986; Govoni et al., 1989).

The king mackerel is a good example of a coastal species in the northern Gulf of Mexico. Fish prey occurred in stomachs of over 95% of adult king mackeral collected off northwest Florida, Louisiana, and Texas and made up over 85% of the total volume of prey consumed (Saloman and Naughton, 1983). Generally, the most common prey were members of the estuarine dependent group. Among invertebrates, which accounted for up to 15% of the volume of prey consumed, the estuarine dependent penaeid shrimps were important. Juvenile king mackerel (100-400 mm FL) also consumed mostly fish prey (92% frequency of occurrence and 89% volume) that were mostly estuarine dependent species (Finucane et al., in press).

Early life stages of mackerel are rather exceptional in that they are almost entirely piscivorous. Larvae and small juveniles (3-23 mm SL) consumed mostly carangids (jacks), sciaenids (croakers), engraulids (anchovies), and clupeids (herrings). Similar to adults, the prey families are mostly estuarine dependent groups although a coastal group (Carangidae) is the most frequently consumed (Finucane et al., in press).

Locations where prey are concentrated could be important microhabitats offering conditions favoring growth, survival and recruitment of larvae of coastal species. For example, ichthyo-plankton and macrozooplankton are concentrated in the frontal waters of the Mississippi River discharge plume (Govoni et al., 1989), and larval and small juvenile king mackerel appear to grow faster in the vicinity of the plume (DeVries and Grimes, 1989). Faster growth can lead to greater survival and recruitment provided survival gains due to faster growth are not offset by increased mortality from predation.

Reef Species

Reef fish occupy hard substrates scattered across the continental shelf from northwest Florida to Texas. Reef fauna constitute the most speciose and ecologically complex of marine communities. For example, continental reef fish communities off North Carolina and South Carolina include 200 species (Grimes et al., 1982).

Reef communities occur in clear shelf waters on outcropped sedimentary rocks richly overgrown by sponges, sea fans, soft and hard corals, and hermatypic corals. Most complete their life cycle on the shelf, with juveniles frequently found on the shallower portion of the shelf (Grimes et al., 1982). Some evidence suggests that a few species (e.g., gag and grey snapper) may be estuarine dependent (Keener et al., 1988).

Adults of the red snapper, *Lutjanidae campechanus* are high trophic level carnivores. Snapper larvae are rarely encountered in

plankton surveys and little is known about the ecology of the young. Spawning is thought to occur over reefs and rock outcroppings (Grimes, 1987) of the mid- to outer-continental shelf (Powles, 1977; Houde et al., 1979). It is not clear if larvae are retained near their natal reefs by eddy-like circulation or are transported into and out of the area by major ocean currents (Powles, 1977).

Diet and feeding ecology of red snapper larvae are unkown although Richards and Saksena (1980) successfully reared larvae of *L. griseus* in the laboratory on a diet consisting of 35-73 μm and 73-110 μm wild zooplankton.

Once juvenile red snapper settle they begin to prefer benthic foods associated with the reef or nearby flats. Juveniles began to eat larger demersal prey by 100 mm FL (Bradley and Bryan, 1976). Shrimp occur in the diet of juveniles year round (Camber, 1955). Squids and octopus, as well as a wide variety of other mollusks, crustaceans and fishes are reported in the diet of juvenile snappers. Adults become exclusively benthic carnivores, feeding upon shrimp, small reef fish, crabs and gastropods, and occasionally tunicates (e.g., Bradley and Bryan, 1976; Futch and Bruger, 1976).

Oceanic Species

The oceanic group of fishes consists of large pelagic species that are top carnivores of oceanic ecosystems. Long range migrations, some even transoceanic, are common to all members. Fast growth, especially during early life, is typical. Many species school as juveniles and young adults but become solitary at older ages. Many oceanic species probably congregate for spawning along prominent oceanographic features (e.g., oceanic fronts) where conditions promote higher productivity, providing food for both adults and larvae alike. The principal fishes in this group are the tunas including bluefin, yellowfin, albacore, bigeye, and skipjack tuna, billfish, swordfish including blue and white marlin and sailfish, and sharks.

Oceanic species could be excluded from this discussion because their life cycles are thought to be largely restricted to oceanic ecosystems. While this is accurate for most members of this group, the yellowfin tuna, *Thunnus albacares*, may be an exception. There is little or no evidence from adults that spawning occurs in the Gulf of Mexico (Erdman, 1968; Goldberg and Herring-Dyal, 1981) and until recently few young stages (<50) had been collected in the Gulf of Mexico (e.g., Klawe and Schimada, 1959; Kelley et al., 1985). However, in 1987, 978 and 131 larvae provisionally identified as yellowfin tuna (Grimes et al., unpublished data; Shaw, unpublished data) were collected during research cruises in the discharge plume of the Mississippi River. Preliminary analyses of these data show that the most and largest larvae were associated with frontal waters of the

Mississippi discharge plume and that larvae were consuming mainly zooplankton prey (Grimes et al., unpublished data). These results suggest that at least this one oceanic species has an important connection to coastal processes and trophic pathways.

Adult yellowfin tuna are high trophic level carnivores on both vertebrate and invertebrate prey; invertebrates (85%) and fishes (77%) occur in the diet in about equal frequencies (Manooch and Mason, 1983). Invertebrate prey were mainly cephalopods and crustaceans; the latter being most often represented by large larvae such as megalopae. Overall diets suggest they are fast aggressive predators that also use their gill apparatus to strain small near-surface organisms from the sea.

Summary

Biological productivity in the northern Gulf of Mexico is dominated by discharge from the Mississippi River system. Annual discharge is approximately 10% of the volume of water on the entire Louisiana/Texas shelf, and much of this discharge is transported along shore in a westerly direction. High nutrient concentrations, for example >100 μmol l^{-1} NO_3, in river water in conjunction with the apparent small impact of nutrients from slope/shelf exchanges, further increase the biological impact of the river.

Waters of the northern Gulf of Mexico are characterized by strong fronts: at the boundaries between river plumes and receiving waters; at the boundary between the Coastal Boundary Layer and the mid-shelf water; and at the boundary between the waters of the outer shelf and the open Gulf. Cross frontal exchanges are not well understood.

Phytoplankton production and stocks within the region of the river plumes are high, often >5 mg C m^{-2} d^{-1} and >300 mg Chl m^{-2}, but models incorporating only nutrients and light indicate stocks are further limited by some combination of grazing, sinking, and advection.

Preliminary summertime measurements of microzooplankton grazing indicate it is a significant source of mortality for phytoplankton; between 35% and 60% of phytoplankton stock d^{-1}. Furthermore, measurements of grazing by the macrozooplankton community indicate an additional 20-30% of the stock is taken by these organisms on some occasions. Fall and winter grazing rates appear to be lower.

There is little available information on sinking fluxes but deposition rates near the Mississippi River Delta are high, between 1 and 2 cm mo^{-1}. Long-term burial rates are about 10% of deposition rates indicating significant resuspension, transport or remineralization.

Measured nutrient fluxes from the bottom to the water column near the Mississippi River Delta are high.

Fisheries production in the northern Gulf of Mexico is high. For example, the region supports the largest volume fishery in the U. S., the gulf menhanden *Brevoortia patronus*. Recruitment is apparently enhanced by the Mississippi River plume fronts and by the abundance of estuarine habitat in this region. Coastal, reef, and even some oceanic fish species are also abundant in the northern Gulf of Mexico.

Acknowledgments

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Food Chains, Yields, Models, and Management of Large Marine Ecosystems

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Chapter 4, Continental Shelf Food Chains of the Northern Gulf of Mexico